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LETTER

Biodiversity loss underlies the dilution effect of biodiversity

Fletcher W. Halliday,^{1*}  Jason
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Laine^{1,3} 

Abstract

The dilution effect predicts increasing biodiversity to reduce the risk of infection, but the generality of this effect remains unresolved. Because biodiversity loss generates predictable changes in host community competence, we hypothesised that biodiversity loss might drive the dilution effect. We tested this hypothesis by reanalysing four previously published meta-analyses that came to contradictory conclusions regarding generality of the dilution effect. In the context of biodiversity loss, our analyses revealed a unifying pattern: dilution effects were inconsistently observed for natural biodiversity gradients, but were commonly observed for biodiversity gradients generated by disturbances causing losses of biodiversity. Incorporating biodiversity loss into tests of generality of the dilution effect further indicated that scale-dependency may strengthen the dilution effect only when biodiversity gradients are driven by biodiversity loss. Together, these results help to resolve one of the most contentious issues in disease ecology: the generality of the dilution effect.

Keywords

biodiversity, community structure, dilution effect, parasitism.

Ecology Letters (2020) **23**: 1611–1622

INTRODUCTION

Increasing biodiversity is often associated with a reduction in the risk of infectious diseases, a phenomenon known as the dilution effect (Keesing *et al.*, 2006, 2010; Civitello *et al.*, 2015; Halliday and Rohr, 2019). Yet, despite more than three decades of empirical research, meta-analyses, reviews, and syntheses, there remains polarising debate regarding the generality of this effect (Halsey, 2019; Rohr *et al.*, 2020). A considerable body of research, initially grounded in pioneering studies of Lyme Disease (e.g., Allan *et al.* 2003; LoGiudice *et al.* 2003; Ostfeld & LoGiudice 2003), and later extended to other systems (e.g., Keesing *et al.* 2006, 2010; Ostfeld & Keesing 2012; Johnson *et al.* 2013, 2019; Joseph *et al.* 2013; Mihaljevic *et al.* 2014; Strauss *et al.* 2016; Liu *et al.* 2018; Halliday *et al.* 2019), provides a promising framework for resolving this debate, suggesting that changes in the structure of host communities, rather than biodiversity *per se*, can explain when a dilution effect should be observed. A commonality among these studies is a focus on biodiversity loss: the structure of host communities often shifts predictably when biodiversity is lost or recovered, particularly following disturbances, and often in a way that favours species with combinations of physiological traits associated with increased disease risk (LoGiudice *et al.* 2003; Ostfeld & LoGiudice 2003; Joseph *et al.*, 2013; Mihaljevic *et al.*, 2014; Johnson *et al.*, 2015a). These predictable shifts suggest that there should be a strong relationship between biodiversity and disease risk following a loss of biodiversity. In contrast, such predictable changes are not expected over natural biodiversity gradients (Table 1).

While many studies focus on measuring the diversity of host species in the context of disease, the structure of host communities can also be measured in the context of disease using characteristics of host species or host functional traits (Johnson *et al.*, 2013; Halliday *et al.*, 2019; Kirk *et al.*, 2019), resulting in trait-based measures of host community competence (Stewart Merrill and Johnson, 2020). This approach, which has rapidly gained traction in disease ecology, suggests that host species that are the best able to spread diseases (i.e., the most competent hosts), often share particular suites of physiological traits (Huang *et al.*, 2013; Martin *et al.*, 2019; Becker and Han, 2020). Thus, host community competence can be linked to distributions of important host traits across host communities (Johnson *et al.*, 2015b; Liu *et al.*, 2017). Importantly, several recent studies indicate that host community competence often covaries with host diversity, obscuring the true effect of host diversity, *per se*, on infectious disease risk (Johnson *et al.*, 2015a; Young *et al.*, 2017; Halliday *et al.*, 2019). This covariance in host community competence and host diversity might, in turn, be driven by community disassembly or recolonisation associated with biodiversity loss (Johnson *et al.*, 2019; Rohr *et al.*, 2020).

We define biodiversity loss as a process through which host species are lost from local assemblages, due to changes in ecological parameters. These changes can be abrupt, such as droughts, fires, floods, and windstorms (Jentsch and White, 2019), or sustained, such as nutrient eutrophication, climate change, and land-use change (Newbold *et al.*, 2015). We contrast this with biodiversity gradients that are not associated with biodiversity loss, but result from differences in the way

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[Correction added on 31 August 2020, after first online publication: First paragraph of the Introduction and Reference list have been updated.]

Table 1 Common drivers of local biodiversity loss and expected impacts on host community structure

	Effect on biodiversity	Effect on community structure and host community competence	Relationship between biodiversity and competence
(A) Drivers of biodiversity gradients associated with biodiversity loss			
Fragmentation	Increasing fragmentation reduces host diversity (Hanski, 2015)	Slow pace of life hosts, which tend to exhibit low competence (Cronin <i>et al.</i> , 2010; Johnson <i>et al.</i> , 2012), and tend to be poor dispersers, are among the first to be lost, while fast pace of life hosts, which tend to also be good dispersers, tend to resist fragmentation (Hanski <i>et al.</i> , 2006; Gibbs and Van Dyck, 2010; Keinath <i>et al.</i> , 2017; Ziv and Davidowitz, 2019). Habitat specialists tend to be lost more commonly than habitat generalists (Keinath <i>et al.</i> , 2017). Parasites that specialise on one or a few hosts also tend to be lost more commonly than host generalists (Colwell <i>et al.</i> , 2012; but see Farrell <i>et al.</i> , 2015).	Negative (i.e., increasing biodiversity is associated with a reduction in host community competence)
Urbanisation	Increasing urbanisation reduces host diversity (McKinney, 2008)	Increasing urbanisation can be considered as a series of filters that select different species (Williams <i>et al.</i> , 2009). Most of these filters appear to favour fast pace-of-life hosts and good dispersers and disfavour slow-pace of life hosts and poor dispersers. For example, urbanisation often increases fragmentation and the frequency and duration of disturbances (Stenhouse, 2004; Hahs <i>et al.</i> , 2009; Ramalho <i>et al.</i> , 2014), which together tend to favour fast pace-of-life hosts (Tilman, 1990; Cadotte, 2007; Keinath <i>et al.</i> , 2017; Lopez <i>et al.</i> , 2018). Urban environmental effects include soil and atmospheric pollution, increased temperatures due to the urban heat island effect, and increased water stress (Pickett <i>et al.</i> , 2001; Grimm <i>et al.</i> , 2008), which also tend to favour hosts with fast-pace-of life and high dispersal abilities (Albrecht and Haider, 2013; Fay <i>et al.</i> , 2015; Merckx <i>et al.</i> , 2018; Heckman <i>et al.</i> , 2019).	Negative
Agricultural intensification	Increasing agricultural intensification reduces host diversity (Beckmann <i>et al.</i> , 2019)	Increasing agricultural intensification fragments host habitat, favouring fast pace of life, and highly competent hosts. Increasing nutrient supplies associated with agricultural intensification also tends to favour hosts with fast-pace-of life and low defence against enemies (Fay <i>et al.</i> , 2015; Heckman <i>et al.</i> , 2019). Similarly, pesticides often disproportionately harm large-bodied, slow-growing (and less competent) hosts (Wagner <i>et al.</i> , 2015), and sublethal pesticide exposure can select for fast-paced life-history strategies (Debecker <i>et al.</i> , 2016), and increase host exposure to parasites by shifting host behaviour (Gendron <i>et al.</i> , 2003).	Negative
(B) Drivers of biodiversity gradients not associated with biodiversity loss			
Environmental heterogeneity	Increasing heterogeneity within communities generally increases host richness (Stein <i>et al.</i> , 2014). Among communities, environmental heterogeneity can generate variation in host diversity, though the direction of the effect depends on the source of heterogeneity (e.g., resource supply, soil type, temperature).	Change in composition is related to the underlying source of heterogeneity. For example, soil resource availability could generate variation based on growth-defence tradeoffs (Heckman <i>et al.</i> , 2019), whereas topographical heterogeneity might be harder to predict (see “Elevation”).	Positive, negative, or none
Island biogeography	Increasing distance and decreasing island size reduces host diversity (MacArthur and Wilson, 1967; Simberloff and Wilson, 1970; MacArthur, 1972)	Increasing distance and decreasing island size favours fast pace-of-life hosts, which also tend to be good dispersers (MacArthur and Wilson, 1967; Hanski <i>et al.</i> , 2006; Gibbs and Van Dyck, 2010; Keinath <i>et al.</i> , 2017; Ziv and Davidowitz, 2019), and might be more competent (Cronin <i>et al.</i> , 2010; Johnson <i>et al.</i> , 2012).	Negative
Elevation	Increasing elevation can increase host diversity, decrease host diversity, or generate unimodal diversity patterns, depending on characteristics of the ecosystem, habitat, host taxonomic group, and their interactions (Körner, 2007; Wohlgemuth <i>et al.</i> , 2008; Altermatt <i>et al.</i> , 2013; Peters <i>et al.</i> , 2016; Laiolo <i>et al.</i> , 2018)	High elevations may favour slow-growing, long lived, well defended (and therefore, less competent) hosts due to limited resources and stressful environmental conditions (Nobis and Schweingruber, 2013). Alternatively, high elevations may favour more competent hosts due to reduced selection for resistance (Pellissier <i>et al.</i> , 2014; Kergunteuil <i>et al.</i> , 2019). Additionally, increasing elevation can change the intensity of biological interactions (Roslin <i>et al.</i> , 2017; Hargreaves <i>et al.</i> , 2019), thereby altering how individual host species contribute to host community competence (Benkman, 2013).	Positive, negative, or none

(continued)

Table 1 (continued)

	Effect on biodiversity	Effect on community structure and host community competence	Relationship between biodiversity and competence
Latitude	Increasing latitude reduces host biodiversity (Wallace 1878, Hillebrand 2004)	Latitudinal gradients of host community structure are often idiosyncratic. For some taxa (e.g., birds), high latitudes favour fast pace-of-life hosts (Jetz <i>et al.</i> , 2008), whereas for other taxa (e.g., some plants) high latitudes appear to favour slow-growing, long lived, well defended (and therefore, less competent) hosts (Oleksyn <i>et al.</i> , 2003). Additionally, increasing latitude can change the intensity of biological interactions (Roslin <i>et al.</i> , 2017; Hargreaves <i>et al.</i> , 2019), thereby altering how individual host species contribute to host community competence (Benkman, 2013).	Positive, negative, or none

that communities assemble based on existing environmental filters (HilleRisLambers *et al.*, 2012) or through ecological drift (Vellend, 2010), including variation in latitude, elevation, environmental heterogeneity, or habitat size. Importantly, the mechanisms through which these processes alter host communities are not mutually exclusive. For example, habitat fragmentation and island biogeography both generate variation in species richness due to changes in habitat size and isolation of habitat patches. The important difference is that habitat fragmentation predominantly changes species richness through the process of community disassembly, whereas island biogeography predominantly changes species richness through the processes of community assembly and ecological drift.

Biodiversity loss can drive the dilution effect because the most competent hosts also tend to be the species that remain or recolonise following biodiversity loss (Table 1A). One explanation for this pattern relates to host life history (Ostfeld and Keesing, 2000; Previtali *et al.*, 2012). Specifically, hosts with life history strategies that favour growth, reproduction, and dispersal, over defence against parasites (e.g., hosts exhibiting a fast pace of life), often contribute the most to disease in the communities that they occupy (i.e., act as disease amplifiers; Cronin *et al.*, 2010; Johnson *et al.*, 2012; Sears *et al.*, 2015). Similarly, in a study of 2277 vertebrate host species and 66 parasites, the best reservoir hosts (those with high abundance and diversity of parasites) were hosts with broad geographic ranges that invest heavily in reproduction and growth (Han *et al.*, 2015b) (see also Luis *et al.*, 2013). These fast pace-of-life hosts are also often the most resistant hosts to extinction (Hanski *et al.*, 2006; Gibbs and Van Dyck, 2010; Albrecht and Haider, 2013; Fay *et al.*, 2015; Keinath *et al.*, 2017; Merckx *et al.*, 2018; Ziv and Davidowitz, 2019). Consequently, as host communities become fragmented or disturbed and biodiversity is lost, these fast pace-of-life, amplifying hosts remain, while their slow pace-of-life counterparts are lost (Joseph *et al.*, 2013; Mihaljevic *et al.*, 2014; Johnson *et al.*, 2015a), leading to covariance between host diversity and host community competence. This hypothesis has been borne out for amphibian (Johnson *et al.*, 2013), mammal (Ostfeld and LoGiudice, 2003), and plant hosts (Liu *et al.*, 2018). In two recent experiments, one using amphibian hosts (Johnson *et al.*, 2019) and the other focused on plant hosts (Liu *et al.*, 2018), dilution was not observed in communities that were disassembled randomly, but when communities

disassembled naturally, biodiversity significantly reduced disease, lending further support to this hypothesis. Consequently, theory suggests that biodiversity gradients associated with biodiversity loss should result in dilution effects.

Whereas biodiversity loss is often linked to increased host community competence during community disassembly, the relationship between natural biodiversity gradients and host community competence is less clearly defined (Table 1B). For example, increasing elevation can increase host diversity, decrease host diversity, or generate unimodal diversity patterns, depending on characteristics of the ecosystem, habitat, host taxonomic group, and their interactions (Körner, 2007; Wohlgemuth *et al.*, 2008; Altermatt *et al.*, 2013; Peters *et al.*, 2016; Laiolo *et al.*, 2018). Similarly, increasing elevation can select for more poorly-defended hosts when there is reduced selection for resistance at high elevations (Pellissier *et al.*, 2014; Kergunteuil *et al.*, 2019), but might also favour slow-growing, long-lived, well-defended hosts due to limited resources and stressful environmental conditions at high elevation (Nobis and Schweingruber, 2013). Consequently using host competence to predict biodiversity-disease relationships along elevational gradients is challenging.

Different drivers of biodiversity gradients might also influence whether and when contingencies arise in the strength and direction of biodiversity-disease relationships (e.g., Halliday and Rohr, 2019). For example, it has been proposed that biodiversity-disease relationships should be strongest at local scales and in tropical regions, where biotic interactions are strongest, and should weaken as spatial scale and (absolute values of) latitude increase and the strength of biotic interactions declines (Wood and Lafferty, 2013; Johnson *et al.*, 2015a; Cohen *et al.*, 2016; Halliday and Rohr, 2019; Liu *et al.*, 2020; Rohr *et al.*, 2020) (but see Magnusson *et al.*, 2020). This effect might be particularly strong among studies that depend on biodiversity loss if biodiversity loss generates consistent patterns of host community competence, and might be weaker or even reverse among studies that do not depend on biodiversity loss depending on the relationship between biodiversity and host community competence (Table 1). Thus, moderation of the dilution effect might differ among studies that do not involve biodiversity loss and among studies that do.

In this study, we test whether the diluting effect of host diversity on disease risk varies between natural biodiversity

gradients and biodiversity gradients that are associated with recent loss of host species. We test this by reanalysing four previously published meta-analyses that came to contradictory conclusions regarding generality in the dilution effect. Re-analysing these data in the context of biodiversity loss reveals a unifying pattern: dilution effects are inconsistently observed for biodiversity gradients that are not associated with the loss of biodiversity (e.g., latitudinal, elevation, and habitat size gradients, or environmental heterogeneity), but are very regularly observed for biodiversity gradients that are generated by disturbances that cause losses of biodiversity (Table 1). These patterns are robust to misclassification of as many as 50% of the biodiversity gradients in these two categories. Incorporating biodiversity loss into tests of generality in the dilution effect further helps to unify understanding of contingencies in the biodiversity–disease relationships, suggesting that scale-dependency should weaken the dilution effect when biodiversity gradients do not involve biodiversity loss, but may strengthen the dilution effect when biodiversity gradients are driven by biodiversity loss. Together, these results help to resolve one of the most contentious issues in disease ecology: the generality of the dilution effect.

METHODS

Does biodiversity loss underlie the dilution effect of biodiversity?

To test whether biodiversity loss can explain generality in the relationship between biodiversity and disease risk, we reanalysed four previously published meta-analyses. These four previously published studies used different selection criteria and modelling frameworks, focused on different subsets of host and parasite taxa, and came to different conclusions regarding the generality

of the dilution effect (Table 2). Conclusions from these published syntheses were contradictory, suggesting that the dilution effect can be robust (Civitello *et al.*, 2015; Magnusson *et al.*, 2020), scale dependent (Halliday and Rohr, 2019), or dependent on latitude, habitat, and parasite life history (Liu *et al.*, 2020).

We obtained data and code (when available) from these four publications. For each study in each dataset, we assigned the driver of the underlying biodiversity gradient, and whether or not that driver was associated with biodiversity loss (presented in Table 1; Table S1) by reading the abstract and methods of each study. We could not identify the driver of biodiversity gradients in five studies (Table 2; Table S1), so those studies were omitted from our analysis. The resulting database from Civitello *et al.* (2015) included 208 effect sizes (Hedge's G) from 45 manuscripts, the database from Halliday and Rohr (2019) included 217 effect sizes (Spearman Rank correlations) from 37 manuscripts, the database from Magnusson *et al.* (2020) included 120 effect sizes (Hedge's G) from 37 manuscripts, and the database from Liu *et al.* (2020) included 136 effect sizes (Fisher's Z) from 20 manuscripts.

The original studies by Civitello *et al.* (2015), Magnusson *et al.* (2020), and Liu *et al.* (2020) were all carried out using a common analytical framework, by performing mixed-effects meta-analyses using the R package metafor (Viechtbauer, 2010). In contrast, Halliday and Rohr (2019) constructed multi-level random effects models using R package lme4 (Bates *et al.*, 2014) to analyse Spearman Rank correlations. So that all four datasets could be analysed using a common statistical framework, we transformed Spearman Rank correlations from Halliday and Rohr (2019) into Fisher's Z following the methods provided in Liu *et al.* (2020). Briefly, the Spearman rank correlation from each study was transformed into Fisher's Z using the following equation: $Z = \frac{1}{2} \ln \left(\frac{1+r}{1-r} \right)$, and the variance of Fisher's Z

Table 2 Summary of key data syntheses studying generality in the relationship between biodiversity and disease risk

	Data types	Studies (unique)	Manuscripts (unique)	Moderators	Contingencies identified	Moderators that interact with biodiversity loss
Civitello <i>et al.</i> , (2015)	All studies	208 (123)	45 (21)	Parasite type, lifecycle, functional group, specialisation; Study type	None	Parasite type
Halliday & Rohr 2019	Studies with more than three unique diversity measures	217 (48)	37 (6)	Spatial scale	Spatial scale	Spatial scale
Magnusson <i>et al.</i> , (2020)	Observational studies	120 (16)	37 (9)	Spatial scale; Latitude; Geographic region	Stronger relationships in temperate regions	Spatial scale
Liu <i>et al.</i> , (2020)	Studies of non-agricultural plant communities	136 (58)	20 (13)	Parasite life history, symptom; Ecosystem type; Study design; Latitude	Ecosystem type; Study design; Parasite life history; Latitude	Parasite life history, symptom; Latitude

Studies correspond to individual relationships between biodiversity and disease risk, with a unique effect size for each study. Manuscripts are the total number of manuscripts from which these effect sizes were calculated. Unique studies and manuscripts are those that were only included in a given meta-analysis. For example, our reanalysis includes 208 effect sizes from Civitello *et al.*, 2015, 85 of which are included in at least one additional meta-analysis, and 123 of which are unique to the Civitello *et al.*, 2015 dataset. Specific details of which manuscripts and studies were included in which dataset can be found in Table S1 and on Figshare (Halliday, 2020), respectively. The column titled, “Moderators that interact with biodiversity loss” summarises the tests of statistical interactions between biodiversity loss and previously-hypothesised moderators of the dilution effect. Figures showing these tests are presented in Figures S1–S3. The following manuscripts were not included because the underlying source of the biodiversity gradient could not be identified: J. N. Mills. Archives of Virology, 45–57 (2005); A.T. Strauss, et al. Ecol Monogr 86(4):393–411, (2016); Zimmermann et al. Acta Parasitologica 62: 493–501 (2017); J. A. Lau, S. Y. Strauss. Ecology 86, 2990–2997 (2005). Sin Nombre Virus from unpublished data in D. J. Salkeld et. al. Ecology Letters 16, 679–686 (2013).

was defined as $V_z = \ln\left(\frac{1}{n-3}\right)$. One study included a Spearman Rank correlation of -1 . We therefore subtracted $1e^{-5}$ from the Spearman Rank correlation when calculating Fisher's Z.

We then performed mixed-effects meta-analyses using Hedge's G values reported in Civitello *et al.* (2015) and Magnusson *et al.* (2020), Fisher's Z values reported in Liu *et al.* (2020), and Fisher's Z transformed from Spearman Rank correlations reported in Halliday and Rohr (2019). Models were constructed in concordance with the methods described in Civitello *et al.* (2015) and Magnusson *et al.* (2020), using the `rma.mv` function in the R package `metafor` (Viechtbauer, 2010). Each model included whether or not the biodiversity gradient was associated with biodiversity loss as a two-level moderator of the dilution effect. Heterogeneity was estimated using restricted maximum likelihood, and separate random intercepts were assigned to the manuscript from which from which effect sizes originated and to parasite species to account for underlying heterogeneity and a lack of independence among effect sizes within a manuscript and across manuscripts that tested the same parasite species. The raw data and an annotated R Markdown script for these analyses are available on Figshare (Halliday, 2020).

Are biodiversity-disease patterns robust to misclassification and whether or not studies included manipulative experiments?

We acknowledge that our classification of biodiversity gradients as being associated with biodiversity loss or not might be imprecise. For example, Rendón-Franco *et al.* (2014) measured diseases of small mammals in three different vegetation types: short grassland, tall grassland, and mesquite shrub, with the aim of acquiring a gradient of host richness and diversity. The factors that determined these three different vegetation types was unclear from the manuscript, so we assigned the driver of this biodiversity gradient as environmental heterogeneity, which is not associated with biodiversity loss (Table 1, Table S1). However, it is equally possible that these three vegetation types were a reflection of different land-use histories, which would be associated with biodiversity loss, and that we therefore misclassified the underlying biodiversity gradient in this study.

To test whether our results were sensitive to misclassification in how we assigned drivers of biodiversity gradients, we randomly selected a proportion of studies, then randomly assigned the driver of biodiversity gradients in those studies, and re-analysed the data, permuting this misclassification analysis 200 times for each misclassification rate.

In addition to problems of misclassification, assigning the underlying driver of biodiversity gradients in experiments can be problematic. Most experimental designs involve some kind of biodiversity loss; however, whether that loss is a random artefact of experimental design or represents a realistic example of biodiversity loss in nature depends on how the experiment is conducted. Consequently, the relationship between biodiversity and disease risk in manipulative experiments is often sensitive to host composition (Venesky *et al.*, 2014; Han *et al.*, 2015a; Halliday *et al.*, 2017). To the best of our knowledge, only two studies have compared random and realistic biodiversity loss experimentally, with both studies finding that

realistic biodiversity loss produced the strongest and most consistent dilution effects (Liu *et al.*, 2018; Johnson *et al.*, 2019). We therefore next dropped experiments from all datasets and re-analysed the data.

The debate surrounding the generality of the dilution effect often involves questions of whether or not it is appropriate to include manipulative experiments in tests of generality (e.g., Halliday and Rohr, 2019; Magnusson *et al.*, 2020). We therefore conducted all remaining analyses on datasets that excluded experiments.

Does accounting for biodiversity loss explain inconsistencies among different data syntheses?

Finally, using the databasets, but excluding experiments, we tested whether inconsistencies among studies in the factors that modify the dilution effect could be explained by biodiversity loss. To this end, we re-analysed the data, using each hypothesised moderator (i.e., explanatory variable) of the dilution effect that was tested in each original meta-analysis (e.g., Parasite life history, Study type, Latitude, Spatial scale, etc.; Table 2) and an interaction between that moderator and whether or not the biodiversity gradient was associated with biodiversity loss. These tests were carried out as mixed-effects meta-analyses using Hedge's G from Civitello *et al.* (2015) and Magnusson *et al.* (2020), Fisher's Z from Liu *et al.* (2020), and Fisher's Z from Halliday and Rohr (2019), using the `rma.mv` function in the R package `metafor`. Heterogeneity was estimated using restricted maximum likelihood, and separate random intercepts were assigned to the manuscript from which from which effect sizes originated and to parasite species to account for underlying heterogeneity and a lack of independence among effect sizes within a manuscript and across manuscripts that tested the same parasite species. The raw data and an annotated R Markdown script for these analyses are available on Figshare (Halliday, 2020).

RESULTS

Our reanalysis of the four previously published datasets revealed that biodiversity gradients associated with biodiversity loss consistently generated dilution effects (Civitello *et al.*: $g = -1.08 \pm 0.15$ [mean \pm SE], $P < 0.0001$; Halliday and Rohr: $Z = -0.29 \pm 0.08$, $P = 0.0002$; Magnusson *et al.*: $g = -0.69 \pm 0.17$, $P < 0.0001$; Liu *et al.*: $Z = -0.32 \pm 0.10$, $P = 0.001$), whereas other biodiversity gradients inconsistently generated dilution effects (Civitello *et al.*: $g = -0.78 \pm 0.37$, $P = 0.036$; Halliday and Rohr: $Z = 0.13 \pm 0.07$, $P = 0.082$; Magnusson *et al.*: $g = -0.29 \pm 0.19$, $P < 0.14$; Liu *et al.*: $Z = -0.28 \pm 0.20$, $P = 0.17$ Fig. 1). These patterns were robust to misclassification of the underlying source of biodiversity gradients in as many as 50% of the studies (Fig. 2). Moreover the patterns were often robust to the exclusion of experimental studies, which can often test contrived community compositions. After excluding experiments in the Civitello *et al.*, Halliday and Rohr, and Magnusson *et al.* datasets, biodiversity gradients associated with biodiversity loss still consistently generated dilution effects ($g = -0.93 \pm 0.22$, $P < 0.0001$; $Z = -0.25 \pm 0.12$,

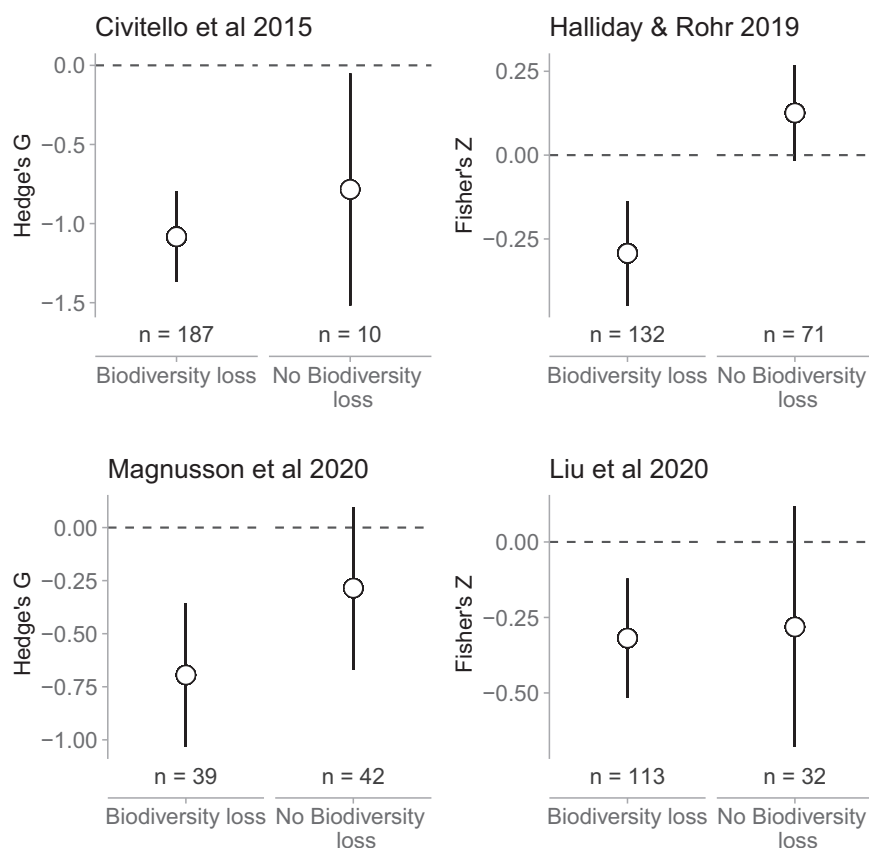


Figure 1 Effect of biodiversity loss on the dilution effect. Each panel corresponds to a separate meta-analysis of the dilution effect. The y-axis is a standardised effect size from the meta-analysis, aimed at estimating the strength of the dilution effect, with values below zero corresponding to a negative effect of biodiversity on disease risk (i.e., dilution). Points are model-estimated means, and error bars are model-estimated 95% confidence intervals. The dilution effect is robust across biodiversity gradients driven by biodiversity loss, but this effect is idiosyncratic across diversity gradients that do not involve biodiversity loss.

$P = 0.042$; $g = -0.69 \pm 0.17$, $P < 0.0001$, respectively), whereas gradients not clearly associated with biodiversity loss still did not ($g = -0.61 \pm 0.33$, $P = 0.07$; $Z = -0.13 \pm 0.08$, $P = 0.12$; $g = -0.29 \pm 0.20$, $P = 0.14$, respectively; Fig. 3). The exception was the Liu database (Table 2; Liu *et al.*, 2020), where there was no significant dilution effect after excluding experiments (Biodiversity loss: $Z = -0.33 \pm 0.21$, $P = 0.12$; No biodiversity loss: $Z = -0.29 \pm 0.27$, $P = 0.28$).

Finally, we tested whether statistical interactions between biodiversity loss and other hypothesised moderators of the dilution effect (e.g., Parasite life history, Study type, Latitude, Spatial scale, etc.) could explain inconsistencies among the four focal studies (Fig. S1–S3). The degree to which the four databases included gradients of biodiversity driven by biodiversity loss versus other factors resolved inconsistencies regarding spatial moderation of the dilution effect, but amplified discrepancies related to latitudinal gradients (Table 2; Fig. 4). Spatial scale significantly interacted with biodiversity loss in both studies that evaluated spatial scale (Halliday and Rohr: estimate = 0.099 ± 0.045 , LRT 5.12, $P = 0.024$; Magnusson *et al.*: estimate = 0.099 ± 0.041 , LRT 6.23, $P = 0.013$); the strength of dilution increased with scale for studies that involved biodiversity loss and weakened with scale for studies that did not (Fig. 4). In contrast to the

consistency across studies in the scale patterns, we found a non-significant (estimate = -0.015 ± 0.011 , LRT 2.40, $P = 0.12$) and significant (estimate = -0.087 ± 0.039 , LRT 5.54, $P = 0.019$) interaction between biodiversity loss and (absolute value of) latitude for the Magnusson *et al.* and Liu *et al.* datasets, respectively (Fig. 4). Moreover the direction of these effects were opposite; in Liu *et al.*, dilution weakened with increasing (absolute values of) latitude for biodiversity-loss studies, whereas in Magnusson *et al.*, dilution strengthened with increasing (absolute values of) latitude for non-biodiversity-loss studies (Fig. 4).

DISCUSSION

This study shows broad evidence that biodiversity loss underlies the dilution effect. The effect of biodiversity loss on the dilution effect was robust to misclassification and whether or not studies included manipulative experiments. Furthermore, accounting for biodiversity loss explained some inconsistencies among prior data syntheses. Together, these results provide important context for understanding the role that biodiversity plays in protecting human wellbeing and ecosystem health, suggesting that preventing biodiversity loss can proactively reduce infectious disease risk (Rohr *et al.*, 2020).

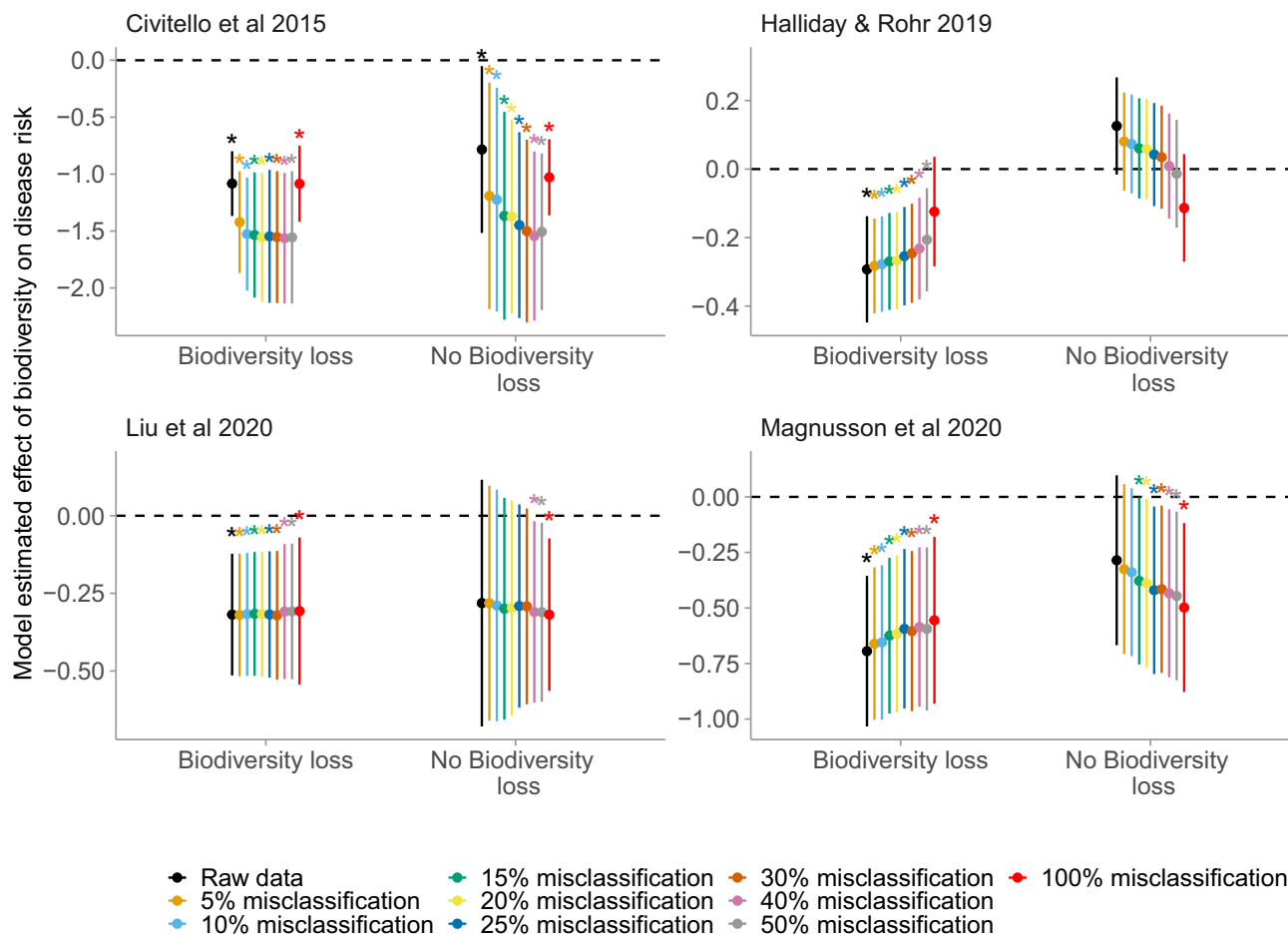


Figure 2 Effect of misclassification on moderation of the dilution effect by biodiversity loss. Each panel corresponds to a separate meta-analysis of the dilution effect. The y-axis is a standardised effect size from the meta-analysis, aimed at estimating the strength of the dilution effect, with values below zero corresponding to a negative effect of biodiversity on disease risk (i.e., dilution). Points are the average model-estimated mean, and error bars are the average model-estimated 95% confidence intervals across 200 simulations. Asterisks correspond to misclassification rates in which the average 95% confidence interval did not overlap zero (i.e., in which tests identified significant dilution or amplification, on average, across the 200 simulations). The effect of biodiversity loss on the strength of the dilution effect is robust to misclassification of at least 10% and up to 50% of studies.

Because community disassembly often favours more competent hosts (Table 1), we expected that biodiversity loss would commonly result in dilution effects. Our reanalysis of four published datasets is consistent with this idea: dilution effects were commonly observed among biodiversity-loss studies across all four datasets. However, we did not directly test whether dilution effects arise due to an increase in competent hosts, because most published studies do not report the identities or abundances of (potentially) diluting host species. Future studies should test for generality in this mechanism directly by comparing host community structure (including traits associated with host community competence and host biodiversity) across a variety of biodiversity drivers (e.g., Halliday *et al.*, 2019), and in a variety of study systems.

Because the relationship between host community competence and biodiversity is often unpredictable along natural biodiversity gradients (Table 1), we expected that gradients not associated with biodiversity loss would inconsistently result in dilution effects. Our results support this idea: dilution effects were inconsistently observed among non-biodiversity-

loss studies in three out of four datasets. However, these results do not suggest that dilution effects only occur when biodiversity gradients are associated with biodiversity loss. Importantly, even when there is no net association between host diversity and community competence, increasing biodiversity can still reduce disease risk of parasites that are specialised to infect a small number of host species by modulating host density (i.e., via encounter reduction; Mitchell *et al.*, 2002; Keesing *et al.*, 2006). Encounter reduction, in turn, might be particularly relevant when gradients include seasonality (e.g., latitude, elevation) that affects peak prevalence and the duration of the epidemic season. Thus, biodiversity gradients that are not associated with biodiversity loss could still generate consistent dilution effects via encounter reduction for specialist parasites. Understanding the degree to which biodiversity influences disease risk among specialists versus generalists in the context of biodiversity loss therefore remains an important topic for future studies.

Our prediction that biodiversity loss underlies the dilution effect was grounded in host community competence, because

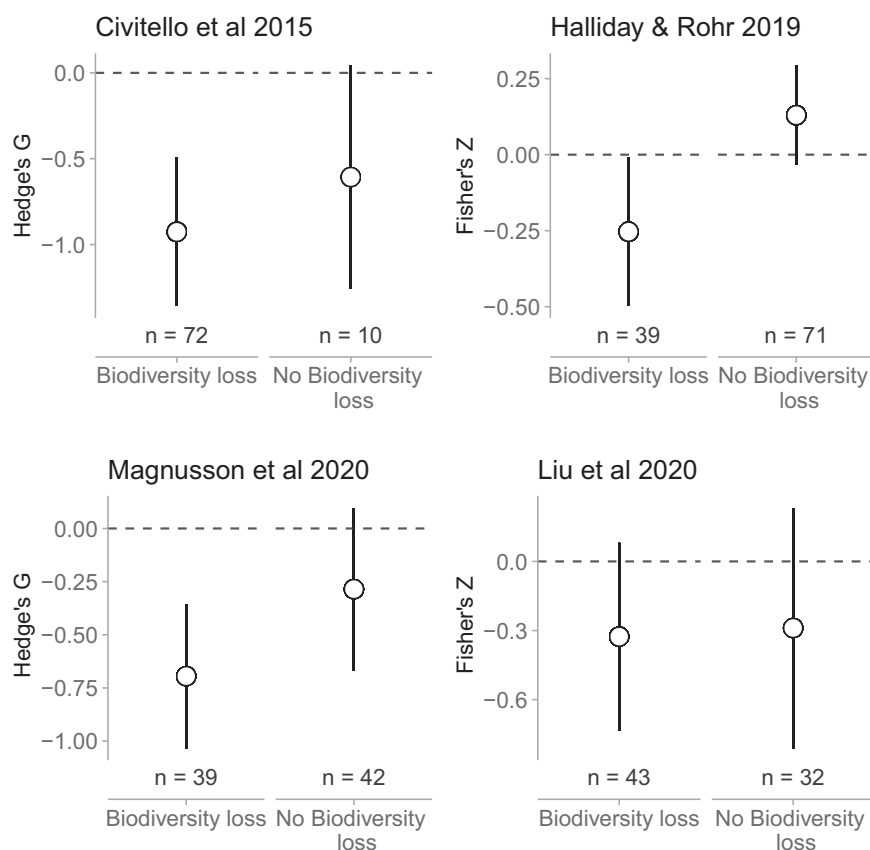


Figure 3 Effect of biodiversity loss on the dilution effect after excluding experiments. Panels correspond to different databases. Y-axes are standardised effect sizes, with values below zero corresponding to negative effects (i.e., dilution). Points are model-estimated means, and error bars are model-estimated 95% confidence intervals. With the exception of Liu, which was sensitive to study design, the dilution effect is robust across biodiversity gradients driven by biodiversity loss, but this effect is idiosyncratic across diversity gradients that do not involve biodiversity loss, even after excluding experiments.

host communities become more competent as biodiversity is lost (e.g., Johnson *et al.*, 2013; Liu *et al.*, 2017); however, biodiversity loss could also influence the dilution effect by other potential mechanisms. As an example, biodiversity loss does not necessarily alter nutrient availability in the same way that nutrient availability influences biodiversity, with implications for higher trophic levels (Grace *et al.*, 2016; Cappelli *et al.*, 2020). Gradients that are or are not associated biodiversity loss could also differ in host abundance or density, connectivity of hosts and parasites, or host temporal turnover (Keesing *et al.*, 2006, 2010; Young *et al.*, 2014; Johnson *et al.*, 2015a).

Our results also suggest that statistical interactions between biodiversity loss and spatial scale might be sufficient to explain inconsistencies among the four focal studies, but that interactions between biodiversity loss and latitude are not. However, as in prior studies on the dilution effect, we wish to emphasise that our analysis of spatial scale might be sensitive to the scarcity of studies conducted at the largest spatial scale and to a variety of study characteristics linked to spatial scale, including the metrics used to estimate diversity and disease, study design, and parasite type (Halliday and Rohr, 2019). Importantly, both datasets that tested spatial scale only included one global study where the underlying gradient involved biodiversity loss (Derne *et al.*, 2011) and only one global study where the underlying gradient did not involve

biodiversity loss (Wood *et al.*, 2017). Consequently, we cannot rule out the possibility that these results could change if future studies filled these research gaps. Nevertheless, incorporating biodiversity loss resolved inconsistencies among studies related to spatial moderation of the dilution effect.

Even among datasets where biodiversity loss interacted with scale or latitude, the direction and magnitude of these interactions were not always consistent with theory. Specifically, theory predicts that increasing spatial scale and (absolute values of) latitude should weaken the dilution effect, because biotic interactions tend to weaken with increasing spatial scale and (absolute values of) latitude (Wood and Lafferty, 2013; Johnson *et al.*, 2015a; Cohen *et al.*, 2016; Halliday and Rohr, 2019; Liu *et al.*, 2020; Rohr *et al.*, 2020) (but see Magnusson *et al.*, 2020). We therefore expected that if host community competence drives the dilution effect (Johnson *et al.*, 2013), and this process occurs more commonly when biodiversity is lost (Table 1), then this moderating effect of latitude and spatial scale would be strongest among biodiversity-loss studies. Consistent with this hypothesis, increasing latitude weakened the dilution effect in biodiversity-loss studies, though this effect was only observed in one dataset (Liu *et al.*, 2020). In contrast, increasing scale increased the strength of the dilution effect among biodiversity-loss studies. We suggest that this result might be more statistical than biological: among

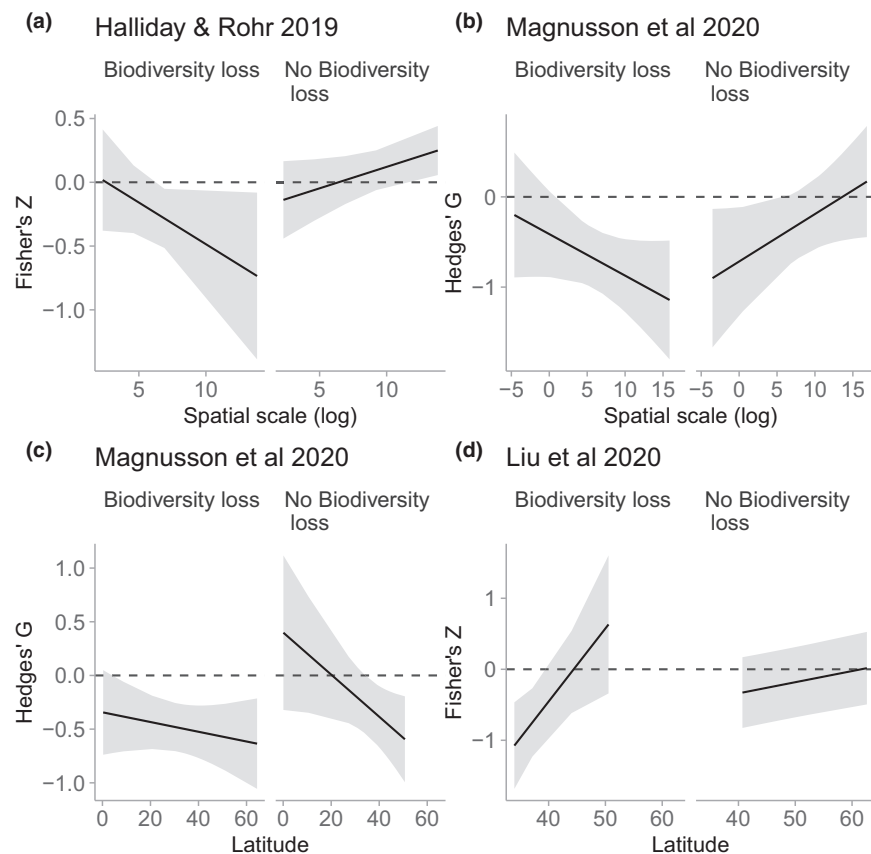


Figure 4 Effect of biodiversity loss on moderation of the dilution effect. Panels correspond to models of the interaction between biodiversity-loss and spatial scale (a and b) or latitude (c and d) for different meta-analyses, excluding experiments. The y-axis is a standardised effect size from the meta-analysis. Lines are model-estimated means, and ribbons are model-estimated 95% confidence intervals. Incorporating biodiversity loss resolves inconsistencies in the effect of spatial scale, but not latitude.

non-biodiversity-loss studies where biodiversity is not associated with host community competence, large spatial scales can confound biodiversity gradients with changes in species pools, weakening dilution effects (Wood and Lafferty, 2013; Rohr *et al.*, 2020). In contrast, among biodiversity-loss studies where biodiversity is associated with community competence regardless of the underlying species pool, increasing scale could strengthen the dilution effect, particularly if large-scale studies capture a larger portion of the biodiversity gradient than smaller-scale studies, and their biodiversity-disease relationships favour dilution over the majority of the gradient (i.e., they are right-skewed; Halliday and Rohr, 2019; Rohr *et al.*, 2020). These results highlight the need for studies that measure biodiversity gradients across spatial scales to better disentangle conditions under which spatial scale and latitude moderate the dilution effect.

This study was not designed to test whether changes in ecological parameters, such as those resulting from anthropogenic factors, cause increasing disease risk *due to* changes in local biodiversity. In other words, this study was not designed to test whether biodiversity loss is an intermediate cause of changes in disease risk. Changes in biodiversity resulting from anthropogenic drivers have been linked to subsequent changes in ecosystem functioning (Hautier *et al.*, 2015). However, anthropogenic drivers do not universally reduce local

biodiversity (Chase *et al.*, 2019; Dornelas *et al.*, 2019), complicating the linkages among anthropogenic drivers, biodiversity loss, and disease risk. Disentangling whether anthropogenic drivers alter disease risk due to changes in species richness, *per se*, is further complicated by delayed impacts of past events, which can interact with existing environmental filters during community reassembly (Jung *et al.* 2019). However, despite these limitations, ecological theory *does* suggest that characteristics of host species that allow those species to resist or rapidly recover following changes in ecological parameters may also make those host species more competent, causing increases in disease risk following such events (Johnson *et al.*, 2013, 2019; Joseph *et al.*, 2013; Mihaljevic *et al.*, 2014; Liu *et al.*, 2018; Halliday *et al.*, 2019). Our results lend some support to this assertion, suggesting that the link between biodiversity and disease risk is strongest when changes in ecological parameters cause biodiversity loss.

Together, the results of this study highlight the need to consider drivers of biodiversity gradients when predicting the role of biodiversity in influencing infectious disease. Specifically, our results suggest that dilution effects may occur less commonly for biodiversity gradients that are not associated with the loss of biodiversity, but occur regularly for biodiversity gradients that are generated by disturbances that cause losses of biodiversity. These results are consistent with a growing

body of literature suggesting that the role of biodiversity in regulating ecosystem processes depends on characteristics of species or individuals present in those ecosystems (Mouillot *et al.*, 2011; Allan *et al.*, 2015; Leitão *et al.*, 2016; Van de Peer *et al.*, 2018; Bagousse-Pinguet *et al.*, 2019; Start and Gilbert, 2019; Heilpern *et al.*, 2020). These results therefore provide clarity in an increasingly polarised debate. Specifically, because characteristics of host communities often predictably change with biodiversity loss, these results suggest that biodiversity loss generally exacerbates infectious disease risk.

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AUTHOR CONTRIBUTIONS

FWH designed the study, analysed the data, and wrote the first draft. All authors contributed substantially to revising the manuscript.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data and code supporting the results are archived on Figshare: <https://dx.doi.org/10.6084/m9.figshare.12155562>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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